

A NEW GENUS OF TRIASSIC DICYNODONT FROM EAST AFRICA AND ITS CLASSIFICATION

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ABSTRACT. A new Triassic dicynodont *Angonisaurus cruickshanki* gen. et sp. nov. from the Manda Formation of Tanzania is described. The specimen is considered to be closely related to *Tetragonias* from the same Formation and belongs to the same family, the Shansiodontidae. The classification of Triassic dicynodonts is reviewed. Using the characteristics of snout shape and length, proportion of preorbital and postorbital region, and degree of obliquity of occiput, most genera are put into the three families Kannemeyeriidae, Stahleckeriidae, and Shansiodontidae, which were suggested by Cox (1965). The criteria for the classification are also discussed.

VERTEBRATE fossils were first found in the Ruhuhu Valley of south-western Tanzania by Stockley in 1930 (Stockley 1932). Further collections were made by German and British workers in the 1930s (Nowack 1937; Parrington 1936), and it became clear that the Permian and Triassic deposits contained a rich fauna. A joint collecting expedition of the British Museum (Natural History) and University of London therefore spent two months in the area in 1963 (Attridge *et al.* 1963). As a result, 450 specimens, weighing 2–3 tons, were collected from the Late Permian and Triassic deposits of the area. The Triassic fossils were found in the eroding land-surface (particularly in the dry stream gullies) of an area between the Mhimbasi and Lipinda streams, which ran northwards into the Rutukira River, itself a tributary of the Ruhuhu River.

The fauna of the Triassic Manda Formation (Charig 1963, 'Upper Bone Bed' of earlier workers) includes the rhynchosaur *Stenaulorhynchus* (von Huene 1938a), trirachodont and traversodont cynodonts (Crompton 1955, 1972), prestosuchid pseudosuchians (von Huene 1938b) and dicynodonts (Cruickshank 1965, 1967). This faunal assemblage suggests that the Manda Formation is of Middle Triassic age, while the similarity between the Manda pseudosuchian *Mandasuchus* and *Ticinosuchus* of Monte San Giorgio, Switzerland, suggests that its age is approximately uppermost Anisian (Cox 1973).

SYSTEMATIC PALAEOLOGY

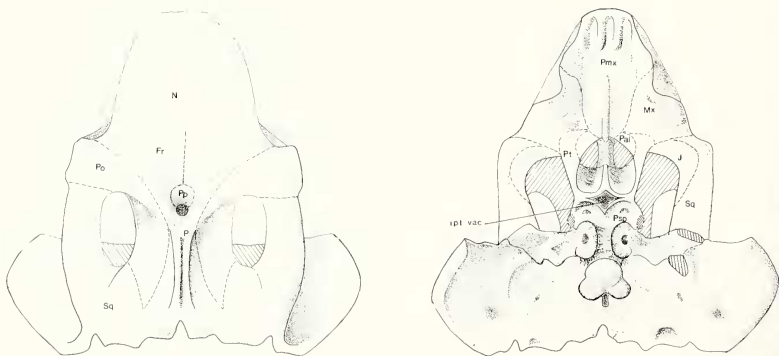
Suborder ANOMODONTIA
Infraorder DICYNODONTIA
Genus *Angonisaurus* gen. nov.

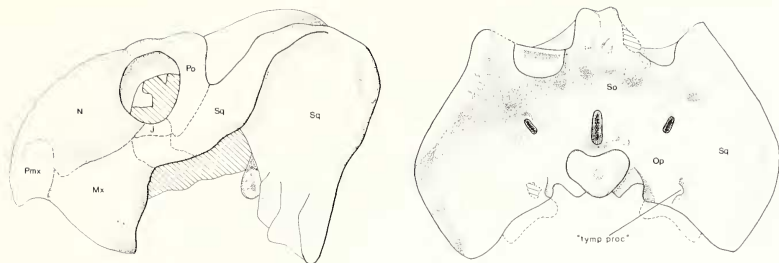
Diagnosis. Skull high, medium size, approximately triangular in dorsal view. Squamosal extends far laterally. Width of skull greater than length. Snout rounded and blunt. Preorbital region short but postorbital region long (about 50 % of the length of the skull). Temporal fenestra large, rectangular. Interorbital bar wide. Intertemporal bar wide ventrally, but tapers upwards to a narrow crest on which a more narrow, deep groove exists. Tuskless, but caniniform process triangular and strong, nasal boss present. Orbits directed laterally. Occiput high and slightly oblique (height is about 65 % of its width), so that the lower jaw is short.

Derivation of name. After the local Tanzanian tribe, the Angoni.

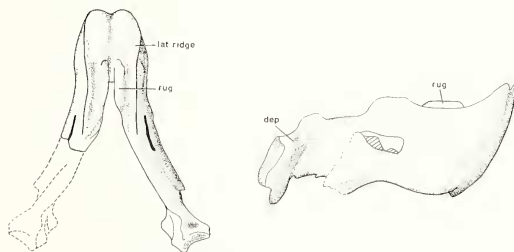
Angonisaurus cruickshanki gen. et sp. nov.

Text-figs. 1-5

Diagnosis. As for genus.*Derivation of name.* In honour of Dr. A. R. I. Cruickshank, who helped to collect the specimen and also prepared it.*Holotype.* Skull, lower jaw, left pectoral and left pelvic girdle, vertebrae, and ribs (field number U12/1: B.M.(N.H.) R 9732).*Locality.* 0.5 km north of the Hita stream-bed, and about 1.7 km south-east of the Rutukira river.*Horizon.* The lowest fossiliferous level in the Manda Formation; Middle Triassic, probably uppermost Anisian.*Description.* The skull is almost complete, but is slightly distorted: the left side of the skull is shortened and the right side is extended, causing deformation of the shape of the orbits and angle of the occipital wing of the squamosal. Only a few parts of the skull are missing.Dorsal view (text-fig. 1*b*). The maximum dimensions of the skull are 30 cm long and 33 cm broad. The pineal foramen lies at the bottom of a deep conical pit which includes also the preparietal bone. This pit also extends posteriorly as a deep groove down the midline of the intertemporal bar, flanked by ridges formed by the postorbitals and parietals. The orbits are directed laterally. The interorbital region is wide (13 cm). It is impossible to trace the sutures in this region because of the massive nature of the bone.Lateral view (text-fig. 2*b*). The skull is tuskleless, but the caniniform process of the maxilla is strong and has a stout, straight posterior edge. There appears to have been a low roughened boss above the external naris but the latter is damaged. The median interorbital ossification called variously the sphenethmoid (Cox 1959) or septosphenoid (Sun 1963) is well preserved. It is in contact with the processus cultriformis, so as to close the front wall of the braincase. The epipterygoid is missing.Palatal view (text-fig. 1*a*). As preserved, the palate is narrow and rectangular. The pterygoid region is damaged, but it is clear that the interpterygoid vacuity is short, as in most Triassic dicynodonts. Two pairs of curved ridges meet anteriorly, posteriorly, and laterally to enclose the interpterygoid vacuity (text-fig. 1*b*, ipt. vac.), which is shaped like a diamond with curved sides. No labial fossa can be seen. The sutures between the basioccipital, basisphenoid, and parasphenoid cannot be distinguished.Occipital view (text-fig. 2*a*). The upper rim of the occiput turns backward strongly to form a distinct flange. The jugular foramen is absent. There is a pair of low bosses slightly dorso-lateral to the exoccipital condyle. TheTEXT-FIG. 1. *Angonisaurus cruickshanki*, type specimen. Skull in dorsal view and palatal view, $\times \frac{1}{3}$. ipt. vac., interpterygoid vacuity.



TEXT-FIG. 2. *Angonisaurus cruickshanki*, type specimen. Skull in lateral view and occipital view, $\times \frac{1}{2}$. 'tym. proc.', tympanic process.

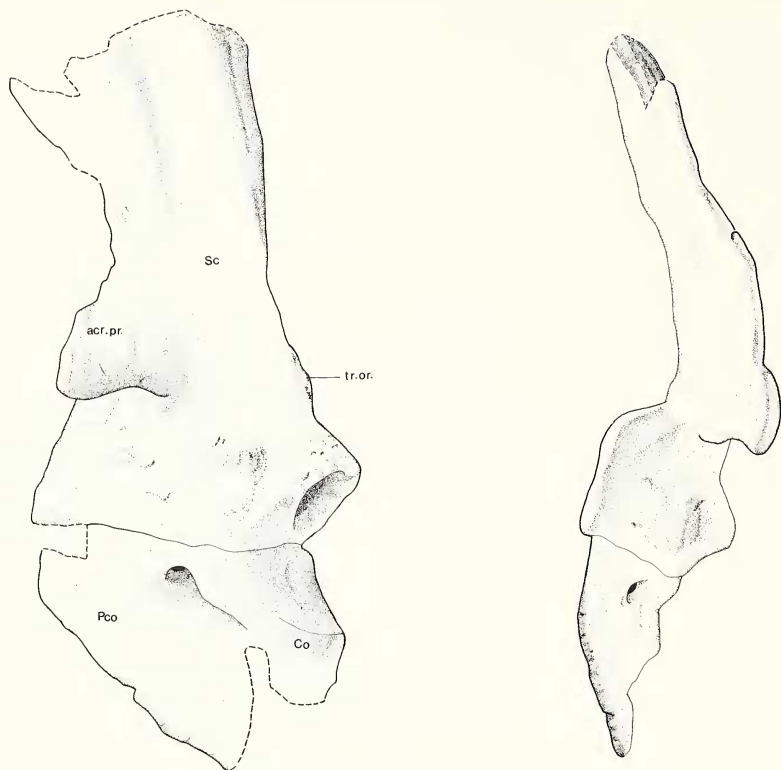


TEXT-FIG. 3. *Angonisaurus cruickshanki*, type specimen. Lower jaw in dorsal and lateral view, $\times \frac{1}{2}$. dep., depression; lat. ridge, lateral ridge; rug., rugosity.

posttemporal fossa is small. The paroccipital process bears a distinct process similar to the 'tympanic process' of *Kingoria* (Cox, 1959). From this process an irregular low ridge extends up to a position lateral to the posttemporal fossa.

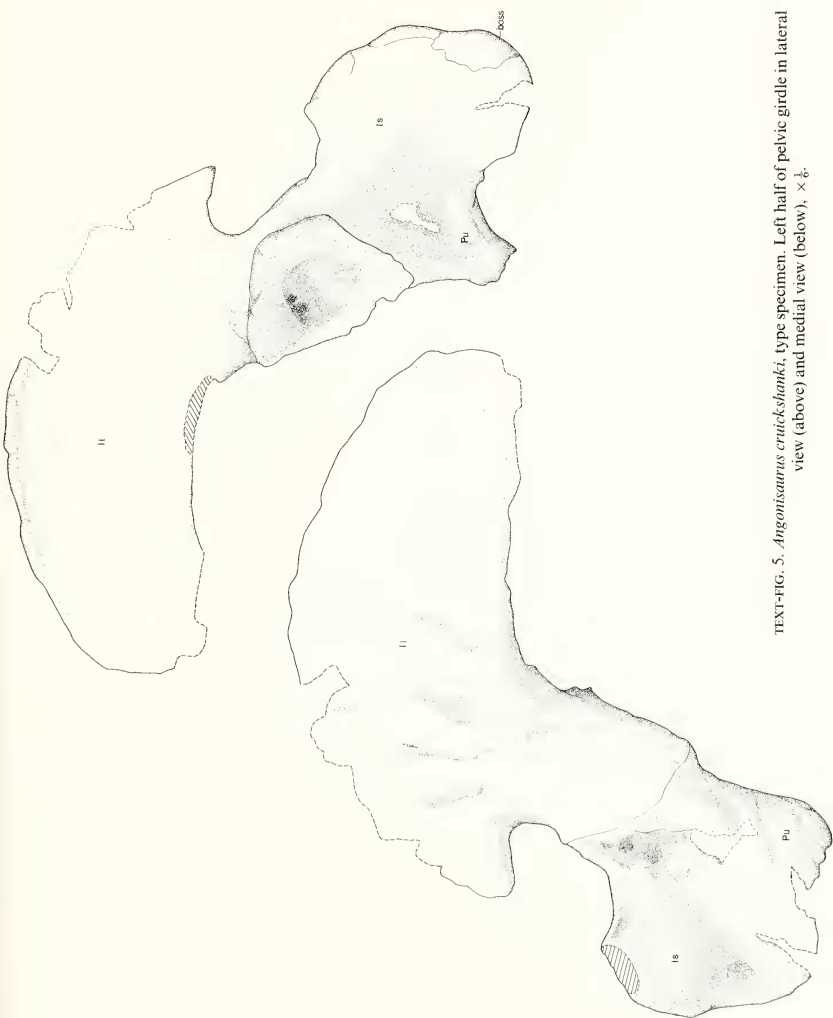
On the left side, the dorsal part of the occiput bears a strong, posteriorly directed process, the end of which is concave. There is some trace of this also on the right side, but the process is smaller and does not have a concave end. It is impossible to tell whether this difference is natural or due to damage, and such a process is unknown in other dicynodonts.

Lower jaw (text-fig. 3). The posterior half of the left ramus of the lower jaw has been lost and the dorsal surface of the right ramus was damaged. The symphyseal region is rectangular in dorsal view, long and deep in lateral view. A pair of lateral dentary ridges turn a little upwards on the tip of beak. A pair of elongate rugosities lies on the inner margin of the dentary rami. The curved articular surface which corresponds with the external condyle is long and smooth. Anterior to it on the upper surface of the lower jaw there is a depression which does not show a smooth surface; this may have received the quadrate when retracted.



TEXT-FIG. 4. *Angonisaurus cruickshanki*, type specimen. Left scapulo-coracoid in lateral view (left) and anterior view (right), $\times \frac{1}{6}$. acr. pr.: acromion process; tr. or.: origin of triceps muscle.

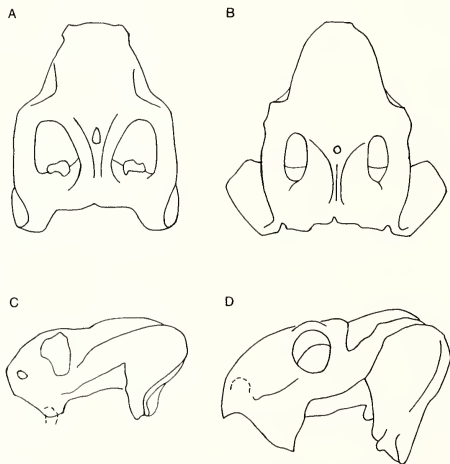
Pectoral girdle (text-fig. 4). The left scapula, clavicle, coracoid, and precoracoid are preserved, but the sternum is missing. The upper part of the scapula is not present; judging from the remaining part, it was rather stout. Its preserved length is 35 cm, the width from its antero-ventral corner to the postero-dorsal corner of the glenoid is 18 cm, and its narrowest width (at the level of the base of the acromion process) is 8 cm. It is slightly curved. The projecting acromion process has a concave distal end. Above the glenoid cavity there is a roughened ridge, running up the length of the bone for 3.5 cm (text-fig. 4, tr. or.). As to the function of this process in the related genus *Tetragonias*, Cruickshank (1967, p. 180) stated: '... At a point level with the acromion, and somewhat on the external face of the bone there is a knob 1 cm high and 1 cm in diameter probably marking the origin of the triceps.' In *Angonisaurus* the process is lower than the level of the base of the acromion. The upper part of the precoracoid and the lower part of the coracoid are damaged. They are fused together, but the suture cannot be traced. The coracoid foramen is small, round and opens downwards in external view.



TEXT-FIG. 5. *Angoniasaurus cruckshanki*, type specimen. Left half of pelvic girdle in lateral view (above) and medial view (below), $\times \frac{1}{2}$.

Pelvic girdle (text-fig. 5.) Only the left ilium, pubis, and ischium are present. The anterior part of the blade of the ilium is extremely expanded, so that this bone is larger than in other dicynodonts. The external surface is smooth and slightly curved, but the internal surface bears several irregular depressions for the attachment of the sacral ribs. The ventral pillar of the ilium is stout. It forms the upper part of the acetabulum, which is large and deep. The pubis and ischium are fused together. Only the anterior margin of the obturator foramen is preserved. The upper part of the ischium faces more dorsally than the lower part; these two surfaces meet at an angle, forming a ridge on the lateral surface. Ventral to the point where this ridge meets the posterior edge of the bone, there is a thickened boss (text-fig. 5, boss), which Cruickshank (1967) suggested may mark a point of muscular attachment. The surfaces where the ilium and pubo-ischiadic plate join together are roughened, and there is no evidence to suggest that there was movement between these two elements.

Discussion. The classification of Triassic dicynodonts in general is dealt with in a later section. For present purposes, it is sufficient to note that in its general shape, and particularly in its bluntly rounded snout, *Angonisauros* is most similar to *Tetragonias* (Cruickshank, 1967). This genus was found in the same area as *Angonisauros*, and the question naturally arises as to whether they represent separate taxa. However, two sets of characteristics distinguish them. First, though the length of the skull is almost identical in the two genera (28.5 cm in *Tetragonias*, 30 cm in *Angonisauros*), the latter genus has a proportionately larger body. *Tetragonias* has a scapula 19 cm in height and an ilium 13.2 cm long, while the corresponding measurements in *Angonisauros* are 35 cm and 38 cm respectively (the postcranial elements were in each case associated with the skull). Though this difference might suggest recognition only at species level, the differences between the skulls seem more profound (text-fig. 6). *Tetragonias* has large maxillary tusks, together with a labial fossa behind the maxilla which presumably provided access for blood vessels, etc., to the root of the tusk. *Angonisauros* lacks both tusks and labial fossa, but instead has a much larger, more ventrally projecting maxilla. The interorbital bar of *Tetragonias* is much narrower than that of *Angonisauros*, and its orbit is comparatively larger. Finally, the squamosals of *Angonisauros* project laterally



TEXT-FIG. 6. Dorsal and lateral views of skulls of *Tetragonias* (left) and *Angonisauros* (right).

much further than those of *Tetragonias*, and its whole preorbital region is much larger. These differences seem sufficient to merit generic recognition, though the two genera are clearly closely related.

FUNCTIONAL ANATOMY

Jaw function. *Angonisauros* is tuskless, and lacks any teeth, but has strong, triangular caniniform processes. Anteriorly, the medial surface of the rim of the palate supports two palatal ridges. The symphyseal region of the lower jaw is long and massive. On the dorsal surface of the dentary it forms a medial, shallow, wide groove, lying between two short dentary tables. On the inner rim of the lower jaw, corresponding to the postcanine teeth, there is a prominent ridge ascending above the surface of the dentary. Lateral to this ridge is a shallow depression in the position of the longitudinal groove of *Lystrosaurus*. The outer rim of the lower jaw is slightly higher than the middle longitudinal depression, but it is not sharp. The anterior ends of the dentary tables turn up to form short, sharp processes. The tip of the lower jaw is not produced upward in the midline, so it forms a median depression between the two lateral processes.

Crompton and Hotton (1967) analysed the movement of the lower jaw in *Lystrosaurus*. They thought that the first step was to protract and elevate the lower jaw, but that it could not complete the jaw closure in this position. Further closure could only take place by retraction of the mandible, which forced the curved posterior end of the jaw progressively downwards against the quadrate. The whole lower jaw was simultaneously swinging about a point on the maxilla, so that its anterior end moved further dorsally to close the gape.

In *Angonisauros* there is a depression just in front of the articular condyles; the surface of this depression is not as smooth as the articular surface. When the lower jaw was in protraction the lateral anterior processes of the mandible were probably in contact with the anterior palatal ridges. Crompton and Hotton (1967) described a similar situation in *Lystrosaurus*. As the jaw approached the retracted position, the square anterior edge of the lower beak passed close to the anterior wall of the palate, its median and antero-lateral processes intermeshing with the ridge and grooves of the palate. So retraction of the lower jaw and simple depression and elevation of it in a retracted position would have produced a cutting action between the ventral edges of the palatal rim and the symphyseal end of the lower jaw.

Cluver (1975) thought that in *Chelydontops* some slicing would very likely have occurred between the lateral sides of the lower jaw beak and the palatal rim, and *Angonisauros* shows the same condition. During the elevation of the lower jaw, the lateral edge of the lower jaw beak passed close to the inner surface of the caniniform process. Although the lateral edge of the mandible is not as sharp as the anterior edge, a slicing action could take place between the horny layers covering them. The resulting increase in the length of the cutting surface would have been a considerable advantage.

As shown above, the animal used the rims of the palate and lower jaw to cut food. Teeth are not present on either the palate or the lower jaw. Although a pair of elongate rugosities lie on the inner rim of the lower jaw, they could not contact the palatal surface, so there was no possibility of a grinding action between them. The masticatory apparatus was essentially one adapted to cutting and not to grinding.

THE TAXONOMIC POSITION OF *ANGONISAURUS* AND THE CLASSIFICATION OF TRIASSIC DICYNODONT

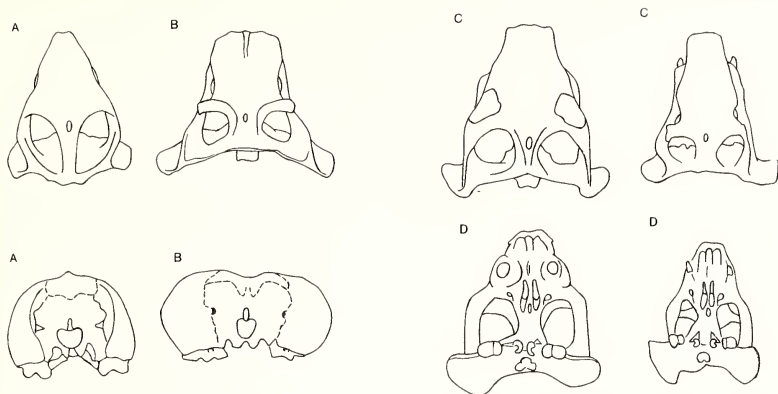
As has already been noted, *Angonisauros* is very similar to *Tetragonias*. The latter genus (then known as '*Dicynodon njalilus*'), together with *Shansiodon* from the Lower Triassic of China, was placed in the family Shansiodontidae by Cox (1965). However, his classification has been criticized by Keyser and Cruickshank (1979), who provide an alternative classification in which these genera are merged into a larger sub-family, the Dinodontosaurinae (see Table 1). These conflicting views must therefore be discussed before the taxonomic position of *Angonisauros* can be decided.

TABLE 1. Two alternative views on the classification of Triassic dicynodonts.

Cox (1965)		Keyser and Cruickshank (1979)	
Family	Kannemeyeriidae	Family	Kannemeyeriidae
	<i>Kannemeyeria</i>	Subfamily	Kannemeyeriinae
	<i>Sinokannemeyeria</i>		<i>Kannemeyeria</i>
	<i>Parakannemeyeria</i>		<i>Uralokannemeyeria</i>
	<i>Ischigualastia</i>		<i>Rabidosaurus</i>
	<i>Placerias</i>		? <i>Rhadiodromus</i>
	<i>Barysoma</i>		? <i>Rhinocerocephalus</i>
			? <i>Sangusaurus</i>
			? <i>Wadiazaurus</i>
		Subfamily	Dinodontosaurinae
			<i>Dinodontosaurus</i>
			<i>Sinokannemeyeria</i>
			<i>Parakannemeyeria</i>
			<i>Dolichuranus</i>
Family	Shansiodontidae		<i>Shansiodon</i>
	<i>Shansiodon</i>		<i>Tetragonias</i>
	' <i>Dicynodon</i> ' <i>njalilus</i>		<i>Vinceria</i>
			<i>Rhinodicynodon</i>
			? <i>Zambiasaurus</i>
Family	Stahleckeriidae	Subfamily	Stahleckerinae
	<i>Stahleckeria</i>		<i>Stahleckeria</i>
	<i>Dinodontosaurus</i>		<i>Ischigualastia</i>
			<i>Placerias</i>
			<i>Barysoma</i>
		Subfamily	Jachalerinae
			<i>Jachaleria</i>

Cox (1965) suggested that most of the Triassic genera could be placed in two families, the Kannemeyeriidae (including *Kannemeyeria* and *Ischigualastia*, among others) and the Stahleckeriidae (including *Stahleckeria* and *Dinodontosaurus*). These two families were distinguished mainly on the shape of the snout and of the occiput. Cox erected a third family, the Shansiodontidae, for two genera (*Shansiodon* and *Tetragonias*, the latter at that time known as '*Dicynodon*' *njalilus*) which did not seem to fit clearly into these two families, which seemed to be more primitive and which, he stated (Cox 1965, p. 507) were 'sufficiently alike for it to be possible, for the present, to take the convenient course of placing them together in a separate family'.

Keyser and Cruickshank (1979) do not believe that the characters used by Cox allow one to distinguish the three separate families that he recognized. Their most fundamental criticism is the opinion that the two South American genera *Stahleckeria* and *Ischigualastia* are so alike that they must be placed in a single Subfamily, not in separate Families as suggested by Cox. They stated (1979, p. 96): 'The skull of *Stahleckeria* has much wider occipital flanges than does *Ischigualastia*, and in the latter genus there is no quadrate foramen and the reflected lamina of the angular contacts the lateral condyle of the lower jaw. Apart from these facts, the differences between the two are hardly more than those used by Cox (1965) and Cruickshank (1967) to demonstrate possible sexual dimorphism in *Dinodontosaurus* and *Tetragonias* respectively' (see text-fig. 7). They show figures (1979, fig. 20) of both genera from anterolaterally and somewhat dorsally, to prove their similarity. But though this particular angle of view minimizes the differences, they can still be seen. It is clear that *Ischigualastia* has a long and narrow intertemporal bar, but it is short and wide in *Stahleckeria*; the dorsal margin of

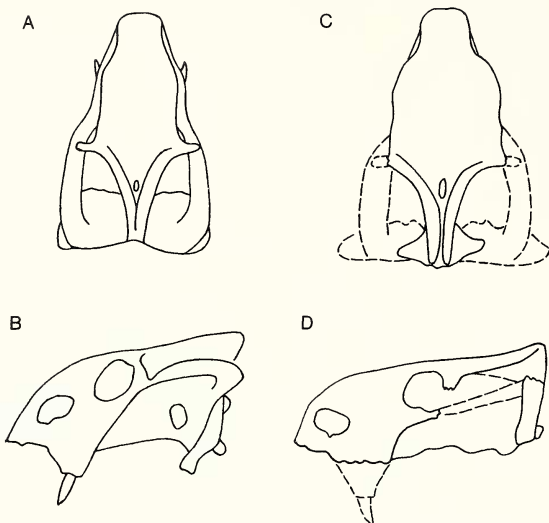


TEXT-FIG. 7. Dorsal and occipital views of skulls of A, *Ischigualastia* (after Cox 1965) B, *Stahleckeria* (after Camp and Welles 1956), C, dorsal views of skulls of presumed male (left) and female (right) of *Dinodontosaurus turpior* (after Cox 1965). D, palatal views of skulls of presumed male (left) and female (right) of *Tetragnostis* (after Cruickshank 1963).

the occiput is convex in the *Ischigualastia* but it is level in the other; the former has a pointed snout, but the latter has a robust one. These characters are presumably correlated with the mechanics of the feeding process, and are therefore far more fundamental than mere sexual dimorphism. They therefore suggest that the two forms are not closely related and, as Cox suggested, *Ischigualastia* and *Stahleckeria* appear to belong in different families.

Keyser and Cruickshank (1979) in criticizing Cox's classification, also discussed the Triassic dicynodont genus *Rechnisaurus*, founded by Roy Chowdhury (1970) on a specimen from India, and placed in the family Stahleckeriidae because of its blunt snout. A second specimen, from Zambia, was described by Crozier (1970), who stated that it differed from the type specimen in having a longer, more pointed snout, and that he believed that the blunt snout of the type was due to fracture or erosion. Keyser and Cruickshank suggest that the true shape of the snout necessitates transference of the genus *Rechnisaurus* to the Kannemeyeriidae and further suggest that it is merely a species of the genus *Kannemeyeria*. Again, since they continue to use the shape of the snout as a criterion for the recognition of separate subfamilies, it is clear that they are only seeking to change the systematic level of distinction involved, rather than implying that the feature has no taxonomic value.

Keyser (1973) had described two new genera of Triassic dicynodont from South-West Africa. He stated that one of them, *Dolichuranus*, had a square, blunt tip to its snout and that it was very close to *Dinodontosaurus*, which Cox (1965) had placed in the family Stahleckeriidae; Keyser assigned *Dolichuranus* to that family. Of the other genus, *Rhopalorhinus*, Keyser (1973, p. 7.) states: 'The specimens probably belong to the family Shansiodontidae (Cox 1965) as is evidenced by the broad snout and nasal bosses and in that the intertemporal bar does not form a very prominent raised crest'—though the features that Cox used to unite the two genera he placed in the family Shansiodontidae were 'a rather short, blunt snout, a fairly narrow interorbital bar, and a very narrow intertemporal bar' (Cox 1965, p. 503). However this may be, a comparison of Keyser's figures of his two genera (text-fig. 8) shows them to be so similar that it is surprising that he found it necessary to place them in different families. It is not, therefore, surprising that further collecting 'made it clear



TEXT-FIG. 8. Dorsal and lateral views of skulls of *Dolichuranus* (left) and *Rhopalorhinus* (right), after Keyser 1973.

that *Dolichuranus* and *Rhopalorhinus* represent the extremes of a morphological series and that the two genera are synonymous' (Keyser and Cruickshank 1979, p. 96).

Though Keyser and Cruickshank (1979) placed *Shansiodon*, *Tetragonias*, and *Vinceria* in their subfamily Dinodontosaurinae, these genera can easily be distinguished from *Dinodontosaurus* in having a short preorbital region and long temporal fenestrae. Keyser (1974) discussed the evolutionary trends in Triassic dicynodonts: increase in total body size; increase in relative length of snout and secondary palate by backward growth of the premaxilla; shortening and dorsal expansion of the intertemporal bar and shortening of the postorbital bones. According to these standards, *Dinodontosaurus* with a large body, a very long preorbital region and short postorbital, should represent a progressive genus, while *Shansiodon* and *Tetragonias* show quite primitive characters. So it is necessary to maintain this group as an independent family, the Shansiodontidae, and *Angoniasaurus*, since it is closely related to *Tetragonias*, clearly also belongs in this family.

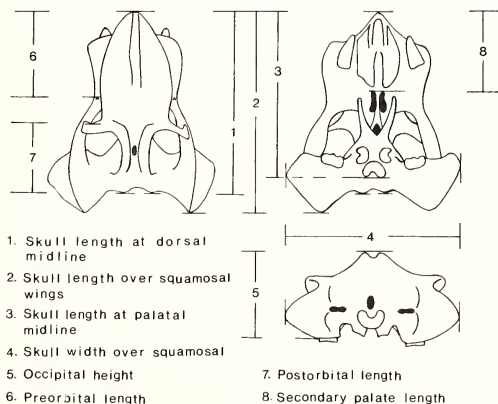
On the other hand, it does appear that the Chinese genera *Sinokannemeyeria* and *Parakannemeyeria*, which Cox placed in his family Kannemeyeriidae, are really closer to *Dinodontosaurus*, as suggested by Sun (1963) (see Table 1). These three genera are alike in having a longer preorbital region with a concomitant shortening of the temporal opening, and a strong, blunt snout. They should therefore be placed in the same group.

Keyser and Cruickshank (1979) also recognize a new sub-family for *Jachaleria* Bonaparte 1971 (which they in error refer to as *Jacheleria*), following Keyser (1974), who based this on the presence of a pterygoid process on the quadrate, and the lower jaw having a very flat profile and long symphyseal region. However, information on these points is often lacking in other genera, and *Jachaleria* itself is so poorly known that it seems best to leave it *incertae sedis*.

Irrespective of the pattern in which the individual Triassic genera are grouped together, Keyser and Cruickshank (1979) also differ in regarding all these genera as belonging to a single family, the Kannemeyeriidae, divided into several subfamilies, rather than these being three separate families as recognized by Cox (1965). However, they conclude that the ancestry of two of these subfamilies lies outside the family Kannemeyeriidae. Their subfamily Kannemeyeriinae is derived from the Permian dicynodont *Dinanomodon*, which similarly has a 'sharply pointed snout', while their subfamily Dinodontosaurinae is derived from the Permian dicynodont *Daptocephalus* which has a 'broad, square-tipped snout'. They show these two lineages as arising in the slightly earlier Permian form *Dicynodon lacerticeps* (Keyser and Cruickshank, 1979, fig. 21). However, as pointed out by Cooper (1980), it is taxonomically unsound for the common ancestor of two subfamilies of a single family to lie outside the family itself. 'Monophyly is the essence of phylogenetic taxonomy and the only objective and natural criterion on which to establish taxonomic categories above the genus level. Thus, Keyser and Cruickshank's interpretation of the Kannemeyeriids merely entirely vindicates Cox's (1965) division of this group into two major families, the Kannemeyeriidae and the Stahleckeriidae' (Cooper 1980, p. 108). Though Cooper himself feels that the *Kannemeyeria*-like and *Stahleckeria*-like forms should be recognized as separate subfamilies rather than families, the main point at issue here is not the taxonomic rank involved but the relationship between the evolutionary relationships and the taxonomic system.

Criteria for the classification of Triassic dicynodonts. The exclusive use of any single characteristic as a basis for classification carries the danger that examples of convergent or parallel evolution may be classified together. It is therefore necessary to base taxonomic diagnoses on as wide a range of characteristics as possible. A number of numerical characters will therefore now be considered in turn. They are defined in text-fig. 9 and documented in Tables 2 and 3. Measurements within brackets were given in the original publications; the remainder are taken from the original text-figures.

Many of the genera documented in these tables have been described since Cox's (1965) classification, as follows, *Elephantosaurus* (Vyushkov, 1969); *Jachaleria* (Bonaparte, 1971); *Moghreberia* (Dutuit, 1980); *Rabidosaurus*, *Rhadiodromus*, and *Rhinodicynodon* (Kalandadze, 1970); *Shaanbeikannemeyeria* (Cheng, 1980); *Sangusaurus* and *Zambiasaurus* (Cox, 1969); *Uralokannemeyeria* (Danilov, 1971); *Vinceria* (Bonaparte, 1969) *Wadiasaurus* (Chowdhury, 1970). Following Keyser and



TEXT-FIG. 9. Cranial features measured (see Tables 2 and 3).

TABLE 2. Skull dimensions of Triassic dicynodonts

	Skull length								
	At dorsal midline	Over squamosal wings	At palatal midline	Skull width over squamosal	Occipital height	Preorbital length	Post-orbital length	Secondary palate length	Lower jaw length
<i>Kannemeyeria cristatrhynchus</i>	328	372	296	316	164	128	124	132	—
<i>K. latifrons</i>	117	129	85	85	50	45	49	36	—
<i>Uralokannemeyeria ypuschkovia</i>	440	473	373	460	186	207	167	173	—
<i>Shanbsikannemeyeria buerdongia</i>	400	—	247	278	133	160(?)	185(?)	143	225
<i>Wadiasaurus indicus</i>	344	400	332	312	196	140	148	128	—
<i>Ischigualastia jenseni</i>	540	—	500	441	320	225	279	189	—
<i>Placerias gigas</i>	582	660	564	492	390	234	258	240	—
<i>Dinodontosaurus turpior</i> (MCZ 1670)	440	472	448	428	240	236	136	164	376
<i>D. turpior</i> (MCZ 1628)	480	536	500	536	276	220	164	208	—
<i>D. brevisrostris</i>	264	300	273	—	—	99	87	99	—
* <i>Chuanaria platiceps</i>	300	330	—	—	—	135	108	—	—
<i>Parokannemeyeria dolichocephala</i>	400	(465)	—	(296)	(220)	(216)	140	—	(345)
<i>Dolichoramus primaeus</i>	345	360	330	240	—	135	147	132	—
<i>Rhinodocynodon gracile</i>	170	200	—	—	—	67	70	—	150
<i>Stahleckeria potens</i>	480	(590)	490	(730)	(320)	208	225	—	(440)
<i>Sinokannemeyeria yingchtaoensis</i>	404	(450)	424	(430)	(180)	(225)	120	168	(360)
<i>Shansiodon wangi</i>	150	180	—	170	100	50	86	—	114
<i>Tetragonias njallus</i>	256	290	242	254	132	74	140	76	190
<i>Angoniasaurus cruckshanki</i>	290	300	258	330	216	96	138	114	220

TABLE 3. Skull proportions of Triassic dicynodonts; all figures are percentages

	Skull breadth + length (total)	Occiput height + breadth	Preorbital length + skull length at midline	Post orbital length + skull length at midline	Secondary palate + skull length	Lower jaw + skull length (total)	Secondary palate + skull length at midline	Skull length at palatal midline + skull length at dorsal midline
<i>Kannemeyeria cristatrhynchus</i>	85	52	39	38	45	—	40	90
<i>K. latifrons</i>	66	59	38	41	42	—	—	73
<i>Uralokannemeyeria vjushkoviya</i>	97	40	47	38	46	—	40	85
<i>Shaanbeikannemeyeria buerdongia</i>	70	48	—	—	58	56	43	62
<i>Wadlissaurus indicus</i>	78	63	41	43	39	—	38	96
<i>Ischigidadastria jenseni</i>	82	73	42	52	38	—	35	93
<i>Placerasaurus gigas</i>	75	79	40	44	43	—	41	97
<i>Dinodontosaurus turpior</i> (MCZ 1670)	91	56	54	31	37	80	37	102
<i>D. turpior</i> (MCZ 1628)	100	51	42	34	41	45	45	104
<i>D. brevisrostris</i>	—	—	38	33	36	—	38	103
* <i>Chanaria platyceps</i>	—	—	45	36	—	—	—	—
<i>Parakannemeyeria dolichocephala</i>	67	74	54	35	—	74	—	—
<i>Dolichuramus primaevus</i>	64	—	39	43	40	—	38	96
<i>Rhodiocynodon gracile</i>	—	—	39	41	—	75	—	—
<i>Stahleckeria potens</i>	124	44	43	47	—	75	—	—
<i>Sinokannemeyeria yingchiaoensis</i>	96	42	56	30	40	80	42	105
<i>Shansiodon wangi</i>	94	59	33	57	—	63	—	—
<i>Tetragonias njatlus</i>	88	52	29	55	31	66	30	94
<i>Angonisauros cruckshanki</i>	110	65	33	48	44	73	38	89

TABLE 2. Skull dimensions of Triassic dicynodonts

	Skull length			Skull width over squamosal	Occipital height	Preorbital length	Post-orbital length	Secondary palate length	Lower jaw length
	At dorsal midline	Over squamosal wings	At palatal midline						
<i>Kamemeyeria cristatrhynchus</i>	328	372	296	316	164	128	124	132	—
<i>K. latifrons</i>	117	129	85	85	50	45	49	36	—
<i>Uralokannemeyeria vjuschkovia</i>	440	473	373	460	186	207	167	173	—
<i>Shaanbeitannemeyeria buerdongia</i>	400	—	247	278	133	160(?)	185(?)	143	225
<i>Waduisaurus indicus</i>	344	400	332	312	196	140	148	128	—
<i>Ischigualastia jensei</i>	540	—	500	441	320	225	279	189	—
<i>Placeras gigas</i>	582	660	564	492	390	234	258	240	—
<i>Dinodontosaurus turpior</i> (MCZ 1670)	440	472	448	428	240	236	136	164	376
<i>D. turpior</i> (MCZ 1628)	480	536	500	536	276	220	164	208	—
<i>D. brevirastris</i>	264	300	273	—	—	99	87	99	—
<i>'Chanaria' platyceps</i>	300	330	—	—	—	135	108	—	—
<i>Parakannemeyeria dolichocephala</i>	400	(465)	—	(296)	(220)	(216)	140	—	(345)
<i>Dolichuramus primaeus</i>	345	360	330	240	—	135	147	132	—
<i>Rhodiocynodon gracile</i>	170	200	—	—	—	67	70	—	150
<i>Stahleckeria potens</i>	480	(590)	490	(730)	(320)	208	225	—	(440)
<i>Sinokannemeyeria yingchaoensis</i>	404	(450)	424	(430)	(180)	(225)	120	168	(360)
<i>Shansiodon wangi</i>	150	180	—	170	100	50	86	—	114
<i>Tetragonomus nyaliths</i>	256	290	242	254	132	74	140	76	190
<i>Angonisauros cruckshanki</i>	290	300	258	330	216	96	138	114	220

TABLE 3. Skull proportions of Triassic dicynodonts; all figures are percentages

	Skull breadth ÷ length (total)	Occiput height ÷ breadth	Preorbital length ÷ skull length at midline	Post orbital length ÷ skull length at midline	Secondary palate ÷ skull palatal length	Lower jaw ÷ skull length (total)	Secondary palate ÷ skull length at midline	Skull length at palatal midline ÷ skull length at dorsal midline
<i>Kamemeyeria cristatrhynchus</i>	85	52	39	38	45	—	40	90
<i>K. latifrons</i>	66	59	38	41	42	—	—	73
<i>Uralokannemeyeria vjuschkovia</i>	97	40	47	38	46	—	40	85
<i>Shaanbeitannemeyeria buerdongia</i>	70	48	—	—	58	56	43	62
<i>Waduisaurus indicus</i>	78	63	41	43	39	—	38	96
<i>Ischigualastia jensei</i>	82	73	42	52	38	—	35	93
<i>Placeras gigas</i>	75	79	40	44	43	—	41	97
<i>Dinodontosaurus turpior</i> (MCZ 1670)	91	56	54	31	37	80	37	102
<i>D. turpior</i> (MCZ 1628)	100	51	42	34	41	—	45	104
<i>D. brevirastris</i>	—	—	38	33	36	—	38	103
<i>'Chanaria' platyceps</i>	—	—	45	36	—	—	—	—
<i>Parakannemeyeria dolichocephala</i>	64	74	54	35	—	74	—	—
<i>Dolichuramus primaeus</i>	67	—	39	43	40	—	38	96
<i>Rhodiocynodon gracile</i>	—	—	39	41	—	75	—	—
<i>Stahleckeria potens</i>	124	44	43	47	—	75	—	—
<i>Sinokannemeyeria yingchaoensis</i>	96	42	56	30	40	80	42	105
<i>Shansiodon wangi</i>	94	59	33	57	—	63	—	—
<i>Tetragonomus nyaliths</i>	88	52	29	55	31	66	30	94
<i>Angonisauros cruckshanki</i>	110	65	33	48	44	73	38	89

Cruikshank (1979), *Rechnisaurus* (Chowdhury, 1970) is included in the genus *Kannemeyeria*, and *Rhopalorhinus* (Keyser, 1973) is included in the genus *Dolichurus* (Keyser, 1973). Following Keyser (1974), *Chanaria* (Cox, 1968) is included in the genus *Dinodontosaurus*. To facilitate comparison, the genera are listed in Table 6 in the systematic position finally accorded to them.

There are a number of possible sources of error in this numerical data. There may be a range of variation within a single species, either during life or resulting from post-mortem deformation. For example, though the type specimen of *Dinodontosaurus turpior* (MCZ No. 1670) has a preorbital length 54% of that of the total skull length (Cox 1965, fig. 14), that of the 'old bull' of the species (MCZ No. 1628) is only 42% (loc. cit., fig. 24), and Cox notes that the type specimen is very unusual in having a 'long, low shape' (1968, p. 10). Apparent differences in skull proportions may also result if different authors have chosen to draw the skull from slightly different angles.

Several different characters have, in the past, been suggested as being useful for taxonomic purposes in Triassic dicynodonts: the width and shape of the snout; the structure and relative length of the snout and secondary palate; the structure and relative length of the intertemporal bar, and the angle between the occiput and the palate. These four suggestions will now be discussed in turn.

Character 1. The significance of the width and shape of the snout has been discussed above, and it has been shown to be a more reliable characteristic than suggested by Keyser and Cruikshank (1979). It should be emphasized in any case that it is the shape of the anterior end of the palatal surface of the premaxilla that is significant, as this is the region used in feeding, rather than the shape of the more dorsal part of the preorbital region. Nevertheless, even this is not always diagnostic; for example, *Wadiasaurus* (Chowdhury 1970) from the Lower Triassic of India, has a palate that tapers anteriorly to a narrow snout but this is flat transversely, not pointed. This characteristic alone is therefore clearly not adequate as a basis for classification.

Character 2. Keyser (1974) suggested that one of the trends in the Triassic dicynodonts was an increase in the relative length of the snout and secondary palate by backward growth of the premaxillae. The ratio between the preorbital length and the total skull midline length is shown in Table 3. In most Permian dicynodonts the preorbital length is only 30–40% of the skull length, and this is also true of a few Triassic genera (*Shansiodon*, *Tetragonias*, *Angoniasaurus*), which have also retained a long temporal opening. In other Triassic genera the preorbital length is 38–56% of the total skull length (see Table 4). As can be seen from Table 3, there is little variation in the relative length of the secondary palate, which usually ranges from 36 to 46% of the total midline skull length; only *Tetragonias* (30%) and *Shaanbeikannemeyeria* (58%) lie outside this range.

Keyser (1974) demonstrated that, concomitant with the elongation of the snout, there is an increase in the length of secondary palate, the extension of which is due to backward growth of the premaxilla. In some genera the prolonged premaxilla contacts the palatine, and the maxilla is excluded from the margin of the choana. But only a few genera show the palatal structure in detail, because of the massive nature of the bones. Thus the premaxilla is known to meet the palatine in *Ischtigualastia*, *Placerias*, *Dinodontosaurus turpior* (MCZ No. 1670), *Dolichurus*, *Stahleckeria*, *Tetragonias*, and *Angoniasaurus*. The two bones are known to be separated in *Kannemeyeria vanhoepeni*, *Wadiasaurus*, *Dinodontosaurus turpior* (MCZ No. 1628) and *Dinodontosaurus brevirostris*. In other forms, the situation is unclear. In any case, the variation within the genus *Dinodontosaurus* shows that this character is not reliable for taxonomic purposes.

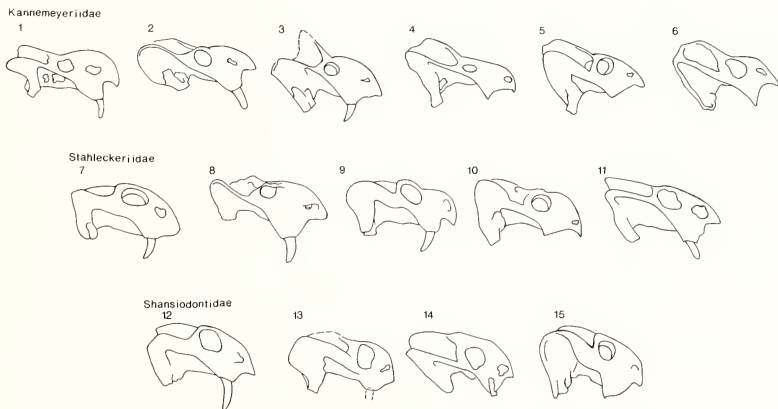
TABLE 4

	Preorbital length ÷ skull midline length (%)	Postorbital length ÷ skull midline length (%)
Stahleckeriidae	38–56	30–43
Kannemeyeriidae	39–47	33–52
Shansiodontidae	29–33	48–57

Character 3. Keyser (1974) also suggested that Triassic dicynodonts show a trend towards a crested, shortened intertemporal bar, and a shortening of the posterior rami of the postorbital bar. (Of course, the proportionate shortening of the intertemporal region is inevitably associated with the proportionate elongation of the preorbital region discussed above; see Table 4). The different genera certainly show considerable variation in each of these characters, but it is not clear that there is any connection between them, nor that any general trends exist. Thus one of the earliest Triassic forms, *Kannemeyeria* of the early Triassic, has one of the shortest, most highly crested intertemporal bars of all the genera, while the later genus *Stahleckeria* has a wide bar without any crest. A wide, short intertemporal bar is also found in *Sinokannemeyeria* of the early Triassic and in *Placerias* of the late Triassic; most other Triassic dicynodonts have an intertemporal bar bearing a longitudinal, narrow crest, though the heights and shapes of the crests vary (text-fig. 10).

The other developing trend mentioned by Keyser (1974), the shortening of the posterior rami of the postorbital bone, does not take place in all the Triassic dicynodonts. Some South American genera (*Dinodontosaurus*, *Ischigualastia*, *Placerias*), and a Russian genus (*Rhinodicynodon*) have a short postorbital, the intertemporal bar consists mainly of the parietal, and the postorbital and squamosal lose their connection. But another group retains the link between the postorbital and squamosal, i.e. *Kannemeyeria*, *Sinokannemeyeria*, *Parakannemeyeria*, and *Dolichuranus*. For this reason Sun (1963) suggested that the Asiatic genera, *Sinokannemeyeria* and *Parakannemeyeria*, had a closer relationship to *Kannemeyeria* than to *Stahleckeria*. But in his original description von Huene (1944, p. 11) stated that in *Stahleckeria* the posterior tongue of the postorbital reaches the transversely extended high edge of the squamosal (Camp 1956, fig. 45 is in error on this feature).

If one combines all the above information on the structure and shape of the intertemporal region, four different patterns emerge: (a) Parietal crest high and narrow; postorbital meets squamosal:



TEXT-FIG. 10. Skulls of Triassic dicynodonts in lateral view, all reduced to the same length. 1, *Kannemeyeria cristarhynchus*, after Keyser and Cruickshank 1979; 2, *Uralokannemeyeria vjushkovi*, after Danilov 1971; 3, *Rabidosaurus cristatus*, after Kalandadze 1970; 4, *Wadiasaurus indicus*, after Chowdhury 1970; 5, *Ischigualastia jenseni*, after Cox 1965; 6, *Placerias gigas*, after Cox 1965; 7, *Dinodontosaurus turpior* after Cox 1968; 8, *Sinokannemeyeria yingchaensis*, after Sun 1963; 9, *Rhinodicynodon gracile*, after Kalandadze 1970; 10, *Stahleckeria potens*, after Camp and Welles 1956; 11, *Dolichuranus primaevus*, after Keyser 1973; 12, *Shansiodon wangi*, after Yeh 1959; 13, *Tetragonias njalilus* after Cruickshank 1967; 14, *Angoniasaurus cruckshanki*.

Kannemeyeria, *Parakannemeyeria*, *Dolichuramus*. (b) Parietal crest narrow but not very high; postorbital does not meet squamosal: *Dinodontosaurus*, *Ischigualastia*, *Rhinodicynodon*. (c) Intertemporal bar wide, does not form a parietal crest; postorbital meets squamosal: *Stahleckeria*, *Sinokannemeyeria*. (d) Intertemporal bar wide, does not form a parietal crest; postorbital does not meet squamosal: *Placerias*.

This analysis does not help to solve the systematic problem. It only demonstrates that it is almost impossible to find any correlation between the length of the temporal fenestra and the form of parietal crest, or between the shape and the structure of the intertemporal bar. After having examined a large collection of *Dinodontosaurus*, Keyser (1974) stated that these specimens showed a great variation in the width of the intertemporal region and that the variation must be attributed to ontogenic variation in the living animals.

Character 4. As first pointed out by Cox (1965), the occiputs of stahleckeriids are almost at right angles to the plane of the palate, while that of kannemeyeriids is more obliquely inclined. Some workers suggested that this obliquity was caused by deformation during preservation, but the regular appearance of an oblique occiput in some families and the existence of a shortened lower jaw, for instance, in *Shaanbeikannemeyeria*, proves that it is a natural condition. This character can be expressed by a ratio of the lower jaw length to the skull length, but in many genera the skull lacks an

TABLE 5. The classification of Triassic dicynodonts

	Skull	Snout	Tusk	Occiput	
Family	<i>Kannemeyeriidae</i>				
	<i>Kannemeyeria</i>	large	medium length, pointed	present	oblique
	<i>Uralokannemeyeria</i>	"	"	"	"
	<i>Shaanbeikannemeyeria</i>	"	"	"	"
	<i>Rabidosaurus</i>	"	"	"	"
	<i>Rhinocerocephalus</i>	"	"	"	"
	<i>Ischigualastia</i>	"	"	absent	slightly oblique
	<i>Placerias</i>	"	"	reduced	oblique
	<i>Moghreberia</i>	"	"	present	"
	<i>Wadiazaurus(?)</i>	"	medium length, flat snout end	absent	"
Family	<i>Stahleckeriidae</i>				
	<i>Dinodontosaurus</i>	large	long, bent, blunt	present	almost vertical
	<i>Parakannemeyeria</i>	"	long, bent, blunt or pointed	"	"
	<i>Dolichuramus</i>	"	long, blunt	"	"
	<i>Rhinodicynodon</i>	medium	blunt	"	"
	<i>Stahleckeria</i>	large	wide and blunt	absent	"
	<i>Sinokannemeyeria</i>	"	long and wide	present	"
	<i>Zambiasaurus</i>	"	blunt	absent	"
Family	<i>Shansiodontidae</i>				
	<i>Shansiodon</i>	medium	short and blunt	present	slightly oblique
	<i>Tetragonias</i>	"	"	"	"
	<i>Angoniasaurus</i>	"	"	absent	"
	<i>Vinceria(?)</i>	large	?	present	oblique
	<i>Incertae sedis</i>				
	<i>Barysoma</i>	large	?	?	?
	<i>Elephantosaurus</i>	"	?	?	?
	<i>Jachaleria</i>	"	?	absent	vertical
	<i>Rhadiodromus</i>	"	?	?	?
	<i>Sangusaurus</i>	"	tapers to blunt point	absent	?